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Molluscs as evolving constructions: necessary aspects for a discussion of their phylogeny

Los moluscos como construcciones en evolución: aspectos necesarios para una discusión sobre su filogenia

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ABSTRACT

A model for the evolution of molluscs is presented. The reconstruction is based on the Frankfurt Theory which conceives organisms as energy transforming hydraulic units which are subject to evolutionary transformation according to the constructional principles ruling organisation. Evolution is reconstructed as a process of constructional transformations in which all stages are explained as explicitly viable constructions; the irreversible transformation phases are also rationally explained by referring to constructional properties of the organismic machines. It is maintained that the predecessors of molluscs must have been elongate worm like animals which were internally tethered by muscles in a way that creeping on the flattened ventral "foot" surface became possible. Only organisms controlling the cross-section by a densely spaced muscle system could start creeping on hard substrate. The establishment of the radula is shown to have been dependent on the adhesive creeping movements which allowed anchorage of the construction to the substrate during rasping. The formation of the shell elements was rendered possible by concentration of motility to the ventral side while the dorsal body wall was held undeformed as a precondition for shell formation. Formation of the muscle grid of the foot on the ventral side of the body and the stabilisation by skeletal elements of the dorsal side caused a shift of the inner organs into a dorsal hump. From the model for the primitive molluscs with segmented shells the continuation into the conchiferan constructions with fused shells and the constructional lineages into the major mollusc constructions are given in captions parallelizing sequences of visualisations of the constructional stages with the major alterations.

RESUMEN

Se presenta un modelo sobre la evolución de los moluscos basado en la Teoría de Frankfurt, que concibe a los organismos como unidades hidráulicas transformadoras de energía sujetas a transformaciones evolutivas de acuerdo con los principios constructivos que regulan la organización. La evolución se reconstruye como un proceso de transformaciones construccionales en el que todos los estados se explican como construcciones explícitamente viables; las fases de transformación irreversibles también se explican racionalmente refiriéndolas a propiedades construccionales de las máquinas orgánicas.

Se defiende que los predecesores de los moluscos deben haber sido animales alargados, tipo gusano, que contaban con una malla muscular interna de tal manera que fuese posible arrastrarse sobre la superficie aplanada ventral del "pie". Sólo aquellos organismos que controlasen su sección mediante un sistema muscular densamente espaciado podían empezar a arrastrarse sobre un sustrato duro.

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La aparición de la rádula se muestra como un proceso dependiente de los movimientos de reptación que permitieron el anclaje de la estructura al sustrato durante el raspado. La formación de elementos conchíferos fue posible por la concentración de la motilidad en la cara ventral mientras que la pared dorsal del cuerpo se mantenía sin deformación, paso previo para la formación de una concha. La aparición de la malla muscular del pie en la cara ventral del cuerpo y la estabilización de la cara dorsal mediante elementos esqueléticos provocaron el traslado de los órganos internos hacia una joroba dorsal. A partir del modelo de moluscos primitivos con conchas segmentadas se presenta el desarrollo hacia construcciones conchíferas con conchas fusionadas y hacia las principales estructuras construccionales de moluscos, mediante encabezamientos de sequencias paralelas de estados de desarrollo, incluyendo las principales alteraciones.

KEY WORDS: Molluscs, hydraulic constructions, phylogenetical reconstruction, metamery, radiation.
PALABRAS CLAVE: moluscos, construcciones hidráulicas, reconstrucción filogenética, metamería, radiación.

INTRODUCTION

Evolution can never be directly observed. It must be reconstructed in models describing the sequences of transformational steps. All stages of evolution necessarily have to be represented by explicitly viable organismic constructions. The theoretical concept and the methodology which allows such reconstructions is the Frankfurt Evolution Theory (FET) (GUTMANN, 1974, 1989; BONIK, GRASSHOFF AND GUTMANN, 1977; GUTMANN AND EDLINGER, 1994a, b, c, d; EDLINGER, 1989a, b; EDLINGER, GUTMANN AND WEINGARTEN, 1991; VOGEL, 1991). In accordance with the demands and results of other biological disciplines, this theory conceives of organisms as energy transforming units and as autoformative constructions. Reconstructions of the evolutionary changes in the sense of the Frankfurt Evolutionary Theory are supported by the insight into the constructional properties of all animal soft body systems which function as hydroskeleton apparatuses and hydraulic units. Before reconstructions are attempted the principles and physical laws governing the organismic entities must be known.

ORGANISMS: ENERGY TRANSFORMING ENTITIES

On the basis of constructional explanations metazoan animals must be described and explained as self-sustaining and energy transforming systems. Basically, they function as machines. They are capable of actively acquiring matter and energy from their environment. By transforming the chemical energy thus obtained into mechanical force the working activity of the body construction is generated.

Energy transformation in the constructions is determined by the structure of specific macromolecular components, mainly in muscles and cilia. To become effective as driving engines the energy transforming structures have to be integrated into an energy cascade of a mechanically coherent structural whole in which the forces are transmitted to mechanically working units. A chain of force transmitting structures connects the energy transforming sites with the working units of the animal body. This chain must never be interrupted because interruption would lead to dysfunction and failure of the organismic construction. The internal activity is also dependent on the form determining structural order and on the effective suppression of useless motoric deformations by restraining structures.

After the chemo-mechanical energy transformation on the macromolecular level the energy is finally utilised in the machinery for the generation of form, locomotion, behaviour, and also for reproduction.

The constructional concept of organisation conceives of organismic units as hydraulic entities that are composed of enclosing membranes and flexible integumental walls. The form of every living body must be enforced by tethering and or bandaging structures which suppress the tendency of all living (hydraulic) units to assume a spherical shape. In animal constructions the form is entirely or mainly determined by the tensile force of muscles and by the mesh of connective tissue structures which are organised in highly ordered arrays. In the course of evolution all transformation stages must be shown to comply with the laws of form-enforcement in hydraulic units. The internal constructional principles and law-like principles determine the directionality and the irreversibility of evolutionary change.

The capability of living constructions to function as energy transforming apparatuses and the ability to obtain an input of matter and energy are determined by the structural order of the energy transforming and working construction. All stages of evolutionary transformation series must never lose their structural order and can only undergo gradual transformation in a way that the preceding constructional stages open up the organismic options of the subsequent alterations. These alterations lead into constructional alleys with further transformation sequences.

Evolution which is driven by the activity of the organisms themselves and the insuppressible generation of non-directional variation has to follow very specific internal principles; the step by step alterations must be forced on alleys of ordered constructions and on sequences of non-fortuitous stages.

Because the principles and laws of organisation can be elucidated in extant organisms, the transitional sequences can be reliably reconstructed. So models can be formulated which are rational in respect to the methodology applied. Consequently they provide valid explanations of the intermediate constructional stages.

In all organismic constructions the course of evolution, mainly of the gross morphological level, can be shown to depend on the constructional organisation outlined above. Consequently all minor physiologically, cytologically, and histologically based functions must be understood as subservient and dependent on the conditions given by the construction as a whole.

Morphological features and so called morphological characters in the traditional sense, at all levels of the organisms, must be seen as enforced by mechanical structures and as energy transforming structures.

Constructional morphology and the reconstruction of evolutionary transformation do not allow the employment of traditional methodologies which prescribe the dismantling and disintegration of living constructions into morphological patterns or an array of distinct characters. Such a procedure is advocated by cladistic "methodologies". Selection and delimitation of features automatically destroys the coherence of organismic systems and the basic hydraulic constitution. In living machines constructional coherence, the hydraulic properties, the order of form-enforcing structures, and the cataract of energy transforming structures of organisms are not accessible to character analysis and comparison of form as advocated by traditional morphology. Only constructional alterations based on the reconstruction of constructionally and functionally viable stages are of interest.

Superficial aspects of similarity of form and so called homologies in the sense of traditional morphology are also of no relevance because constructional explanation has to follow lines of analysis that are comparable to engineering procedures.

Such principles preclude the depiction of fortuitous alterations and arbitrary morphoclines and allow the determination and the reconstruction of the transformation alleys and the establishment of the sequences of stages in the course of evolution. All evolutionary alterations must be shown to be delimited by the internal constructional properties of the living machines (Fig. 1).

Thus, the constructional alterations of evolution have to be reconstructed as

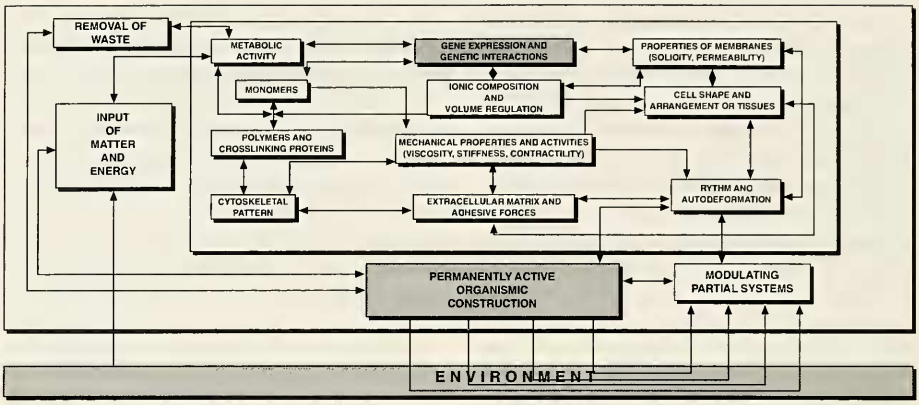

Figure 1. Interrelations between the different levels and parts of organisms and between organisms and their environment (after BEREITER-HAHN, 1991 and EDLINGER, 1995).
Figura 1. Interrelaciones entre los diferentes niveles y partes de organismos y entre los organismos y su medio ambiente (tomado de BEREITER-HAHN, 1991 y EDLINGER, 1995).

internally guided and directed and cannot be understood as adaptational processes or as ruled by environmental factors in the sense of Darwinian thinking. Evolution in the sense of the FET, which is certainly the most radical variant of post-Darwinian concepts assumes a new status and is based on the properties of the evolving organismic entities. Therefore, all Darwinian tenets are excluded from the reconstructions as they are not conducive to the constructional principles which rule organismic constructions and evolutionary transformation.

The theoretical tenets and the methodology of the reconstruction procedures were elaborated by a group of authors (BONIK *ET AL.*, 1977; GUTMANN, 1974, 1989; EDLINGER, 1989A, B, 1991a, b, 1992a, b, 1994a, b; EDLINGER *ET AL.*, 1991; VOGEL, 1991). Numerous models provide corroborating evidence for the successful application of the methods and for the validity of the non-Darwinian evolutionary theory.

On the basis of the just outlined concept ontogenetic and phylogenetic development of molluscs (like that of other "bauplans" of animals) must be reconstructed as transformational sequence of organismic constructions over viable intermediate constructional forms. The sequence of evolutionary alterations must be ruled by the intrinsic laws and constructional principles which are responsible for the continuation of energy transformation and motoric activity in all stages.

MOLLUSCS AS A CASE STUDY

In the following the evolution of the mollusc constructions is presented as a case study. The stages of mollusc evolution have to be described and figured out as tethered systems which in most cases allow flattening of the foot. In this way they can exert sufficient control of body shape by tethering muscles while the shell structures serve only as deformation suppressing elements in the dorsal parts of the coherent whole.

THE DERIVATION OF THE MOLLUSCS: THE KEY TRANSFORMATION STEPS

In reconstructions based on constructional morphology the morphoclines and all aspects of directionality of evolutionary transformation are derived from the biomechanical princi-

ples of the living organisms. Thereby, the arrow of time is firmly supported by irreversible constructional explanation. On the basis of the constructional analysis only the derivation of molluscs from annelid-like forerunners can be consistently explained (GUTMANN, 1974; EDLINGER, 1991a).

The basic mollusc construction must certainly have been a creeping creature with a flattened foot and a dorsal shell or a sequence of shell elements. The problem posed by this basic and only sketchily figured out construction can be formulated in the following way.

How can such a constructional constitution arise in skeleton free hydraulic forerunners of whatever kind of primitive metazoan organisation? Which constructional organisation might have been the incipient stage for the emergence of the basic properties?

The key changes can only be explained if one sets the starting point of the transformation sequence in an annelid like segmented soft body construction which was capable of controlling the cross-section of the body in a way that creeping on a flattened ventral side became possible. Flattening must have been the first stage of adhesive creeping.

The initiation of creeping on a flattened ventral side was a realistic option of annelid-constructions with an internal tethering by dissepimental and other muscles which traversed the cross section of the elongate apparatus.

In conjunction with the development of the adhesively creeping foot and its anchorage at the substratum the radula developed in a well demarcated head region. The use of the radula as a rasping organ was dependent on the concomitant formation of the adhesive creeping foot apparatus. This apparatus allowed the radula indirectly to be pressed against the substratum during feeding. Simultaneously the shells could come into existence as dorsal stabilising structures in the non deformed dorsal portions of the body, while an intensification of motility for peristaltic adhesive creeping occurred on the ventral side. This constructional constitution is in some way still existing in extant flattened chitons.

After the establishment of this construction with its segmented sequence of skeletal structures in polyplacophoran-like organisms new paths of evolution were viable. They led to worm-like constructions in a step by step loss of the shell. In this way some recent forms of worm-like molluscs, the Ventroplicata and the Caudofoveata, are easily derivable from chiton-like predecessors.

Fusion of the shell-plates occurred in the other major branch. Fusion of the segmented shells, in accordance with specific changes of the soft body led to the formation of the conchiferan construction with its typical unified shell.

One consequence of this fusion of the conchiferan shell was that, in conjunction with the formation of the fused shell, a narrow waist developed between the cephalopodium and the dorsal body portion while the internal organs were restructured in the frame of a visceral hump.

The basic conchiferan organisation is to a certain extent represented in the still extant Tryblidiaceans which display clear metamerism of some organs. The basic Conchiferans provided the constructional basis for a radiative explosion that generated most molluscan construction types of the conchiferan level.

The narrowing waist caused and even enforced reductions especially of the of the number of dorsoventral muscles, gills, and kidneys and the compensatory enlargement of the few persisting organs.

The major steps of transformation are described and depicted in the illustrations. The complete explanation of the transitions leading to the mollusc constructions cannot be presented here. It was elaborated in a sequence of papers which may be consulted by the interested and critical reader. In the following the major steps are depicted in the illustrations. The ensuing explanation is formulated as a caption in respect to the illustration (Fig. 2). It should be stressed that the pictures are no typical morphological illustrations.

They present visualisations of the array of form enforcing structures and have to be conceived as constructional models.

(1.1.) A worm-like predecessor (GUTMANN, 1974; EDLINGER, 1991a) with metameric coelomic pouches, dissepiments, and other segmental tethering elements. Flattening is made possible by dorsoventral and other muscles on the dissepiments. All non-longitudinal muscles are helpful in controlling the cross-section and allow flattening of the worm-like body in the incipient stages of creeping on hard substrate.

Metamerism which allowed flattening of the ventral side of the body is mandatory in the precursor stages of molluscs. Flattening of the body is only possible by internal tethering structures such as muscle bearing dissepiments and internal muscles transcending the coelomic chambers which were capable of suppressing the tendency to assume a circular shape. Lack of cross sectional tethering as observed in non-metameric worms would result in a circular cross-section of the soft body and preclude even the beginning creeping on hard substrate.

In an early stage of evolution the mouth became equipped with chitinous teeth which were located around the stomodeum and in the foregut.

(1.2.) Transition to the basic mollusc construction required the formation of a thick ventral muscle lattice forming a flat and highly deformable foot which was able to follow the contours of the bottom. This enabled the organisms to creep adhesively and start rasping at the substrate.

In the course of the incipient stages of transformation the coelom and the other inner organs were shifted to the dorsal side. In the dorsal part of the animals coelomic metamerism was retained and even further demarcated by the newly developing shells.

(1.3.) As muscular activity in the form of peristaltic waves travelling over the foot was concentrated in the ventral portion of the pre-mollusc constructions the dorsal parts of the body were held mostly undeformed. In this situation serial shell elements developed as economising structures; they replaced energetically expensive structures such as muscles and connective tissue structures. The newly developed skeletal structures served as stabilising elements in the deformable and still worm-like hydraulic apparatus. As the shells formed a sequence of independent elements bending movements of the body were still possible; they are remnants of the worm-like bending and peristaltic activity of the predecessors. The dorsally situated serial plates were mechanically connected to the foot by strong muscles which continue to demarcate the preceding metamerism of the annelid-like predecessors.

In accordance with the mechanical requirements for the flattening of the foot the pairs of muscles were arranged as densely spaced pairs of vertical, transverse, and oblique bundles under each plate. These muscles project into the dense muscular grid of the foot. Transversely oriented muscles cross from one side to the other. In this way the form of the whole animal is under control of the tethering structures. Lateral extensions of the shells and their roof-like position allowed the formation of lateral grooves. In these grooves the metameric gills were established as projections of the soft body wall. They were indispensable for the developing molluscs because the adhesion of the foot to the bottom and the covering dorsal shells reduced the body surface usable for respiration. Only the lateral parts of the soft body continued to be exposed to the surrounding medium. The newly developing gills were forced into the old metameric constellation because the vessels had to pass between the pre-existing metameric muscle bundles.

Around the shell a spicule bearing girdle consisting of connective tissue and musculature was established. This girdle served as a protection for the lateral grooves with the gills.

Pari passu with the rearrangement of the musculature the large coelomic cavities of the annelid like ancestors were restrained to a narrow dorsal strip. While the posterior part of the coelom was altered

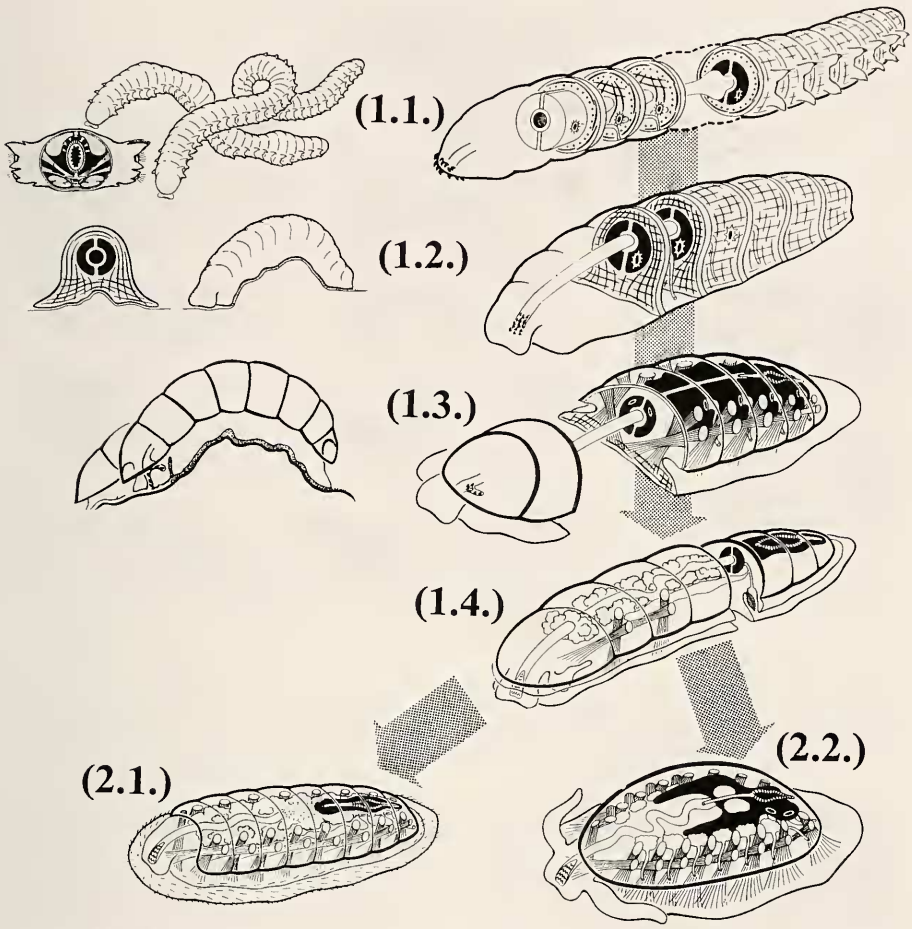

Figure 2. The evolution of chiton-like molluscs out of annelid-like metameric ancestors. An early branching into chiton-like and conchiferan constructions occurs.
Figura 2. Evolución de los moluscos con forma de quitón a partir de ancestros metaméricos tipo anélido. Tiene lugar una pronta separación entre construcciones conchíferas y con forma de quitón.

into the pericardium around the effectively pumping heart the other parts served as cavities containing the gonads.

In conjunction with adhesive creeping the structures around the mouth were perfected into a radula by shifting of the chitinous teeth into a ventral pouch of the foregut. The establishment of the radula must be seen in conjunction with the creeping mode of locomotion. The scraping radula could only become effective when the body remained firmly attached to the substrate in a way that exertion of pressure by the radula onto the substrate would not push the animal body away from the underlying surface. From this follows that the radula could only develop in strict interdependence with the creeping performance of the foot.

(1.4.) Reconstructed predecessors of Conchiferan and Polyplacophoran constructions. In the anterior portion of the body the coelom was gradually reduced. The gut formed lateral pouches in the form of the midgut-glands, which, besides their

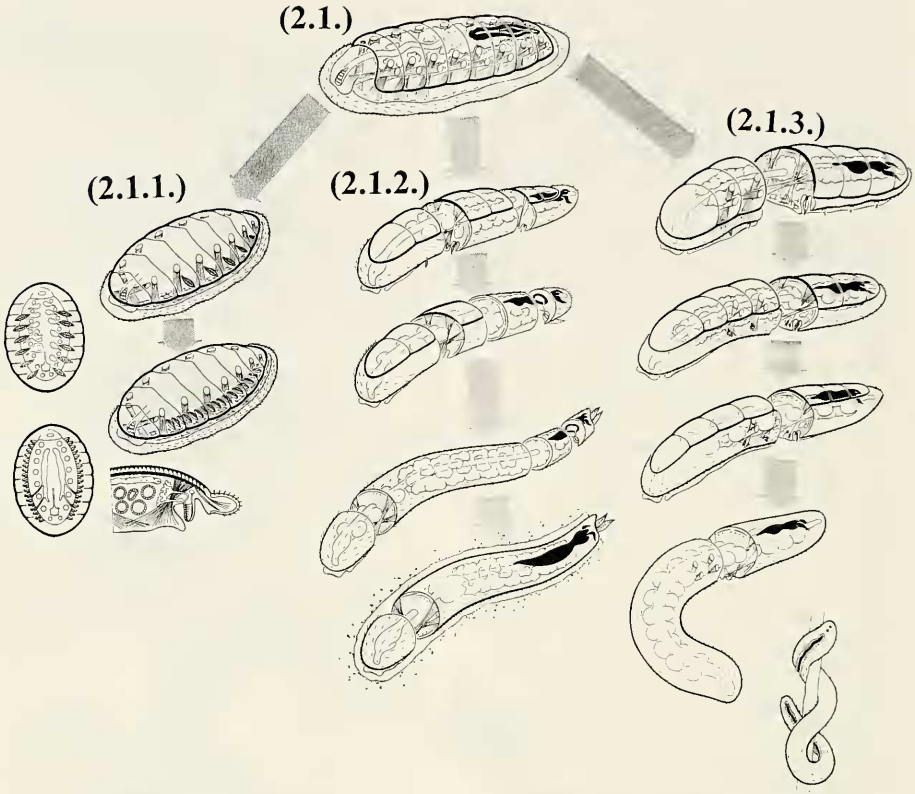

Figure 3. Evolutionary transformation of chiton-like predecessor into Placophora, Caudofoveata and Ventroplicata.
Figura 3. Transformación evolutiva del predecesor tipo quitón en Placophora, Caudofoveata y Ventroplicata.

digestive function, served as newly formed fluid filled entities in the frame of the form enforcing structures and as a substantial part of the filling of the inner spaces of the body. The gut pouches were also helpful in holding the gut in its position. As the coelomic space was restrained by the muscle construction and receded to narrower dorsal cavities glandular kidney structures had to develop as extensions of the metanephridia. They collected excretory material from the extra coelomic spaces mainly in the muscle grid. Such an alteration of the metanephridial excretory organs was necessitated by the enlargement of the extracoelomic fluid fillings of the muscular grid. The coelom inevitably lost its function as the sole fluid filling unit of the body. There can be no doubt that the evolutionary transformation of the muscle apparatus and the restructuring of the excretory system were coupled and mutually dependent.

(2.1.) The Polyplacophoran like transitional stage. The model represents an early organisational constellation in molluscan evolution. These forms retained the metameric organisation of muscle system, shell arrangement, gills, and kidneys (Fig. 3).

(2.1.1.) The fully developed Polyplacophoran constructions represent a side

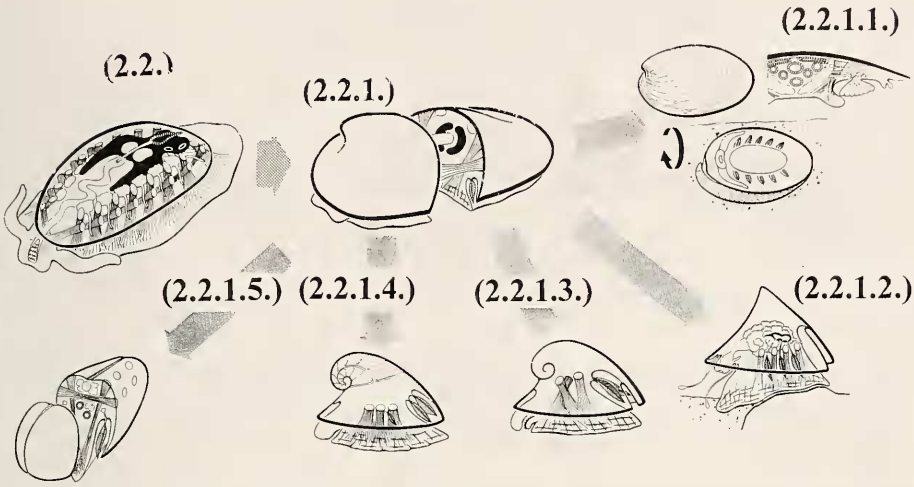

Figure 4. The radiation of conchiferan constructions resulting in diverging organismic types which are capable of occupying different environmental conditions.
Figura 4. Radiación de construcciones conchíferas que resulta en tipos de organismos divergentes capaces de ocupar diferentes condiciones ambientales.

branch of primitive molluscs. Flattening of the shells became more pronounced. The serial shell plates continue to preserve the metameric arrangement of the dorsoventral musculature. In the course of flattening the circulatory and the gill systems were restructured in a way allowing the nonmetameric array of the gills and decoupling of internal metamerism and gill-position. This is unique in Polyplacophorans and not representative for the transition to the molluscs with fused shells.

(2.1.2.) Evolution of the Caudofoveatan construction is part of a radiative differentiation of the polyplacophoran organization. This lineage must have started from polyplacophoran forms (EDLINGER, 1989b) which underwent reduction of the shells. Concomitantly with shell reduction the lattice-like muscle foot was only retained in the anterior portion of the worm like body. The gut was also considerably altered; in the rear portion the intestinal canal was surrounded by the midgut-glands, which held the gut in its position. In these burrowing constructions only one posterior pair of gills was retained in the hind part of the body. The resulting worm-like form developed independently of the Ventroplicatan constructions.

(2.1.3.) Evolution of the Ventroplicatan construction is also a branch of Polyplacophoran radiation: loss of shell structures in conjunction with an enlargement of the girdle resulted in the formation of a worm-like body. The foot-complex persisted as a narrow groove running along the ventral side of the whole body length. The groove remains internally tethered by the dorsoventral muscle bundles which are certainly rudiments of the serial shell related retractors. In contrast to the burrowing Caudofoveata the Ventroplicata are capable of climbing in "tree-like" environments. To corroborate the derivation of the worm-like forms from Polyplacophorans it should be kept in mind that some extant Polyplacophorans as *Cryptoplax* show an observable tendency to reduce the shells.

(2.2.) In the evolutionary alley to the Conchiferan constructions (Fig. 4) the Monoplacophorans demarcate a strategic intermediate stage.

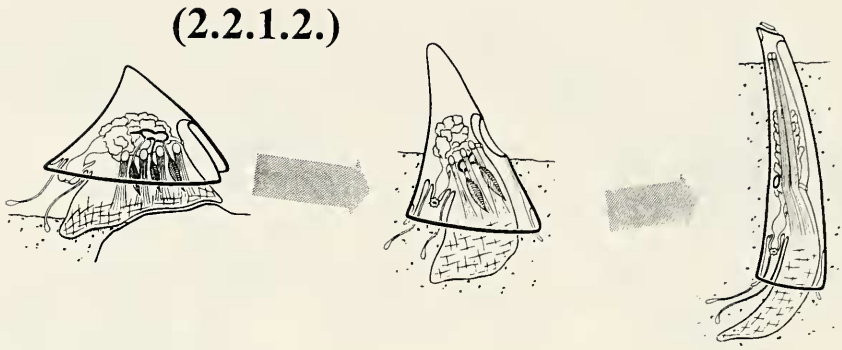

Figure 5. Transformation of monoplacophoran-like ancestors into scaphopods by extreme dorsoventral elongation.
Figura 5. Transformación de ancestros tipo monoplacóforo en escafópodos mediante una elongación dorsoventral extrema.

The unified shell was formed by fusion of the segmental skeletal elements. This process ensued in the deepening of the groove between the cephalopodium and the shell-covered visceral hump. The waist became more pronounced and thereby the cephalopodium was rendered more flexible in respect to the shell. In the Monoplacophora the metameric soft body organization of muscles, gills, nephridia and portions of the coelom is still retained. Metamerism is obviously fading from the rostral portion of the body (GUTMANN, 1974; EDLINGER, 1991a). Noticeable is the concentration of the ancestral structures, coelom, sac bearing nephridia, and gills in the rear part of the body. This situation is indicative of the transition to the other conchiferan constructions which sprang from a radiative divergence of constructions.

(2.2.1.) The fully developed Conchiferan Constructions.

In all conchiferan constructions with fused shells the separation of the two body-portions, the cephalopodium and the dorsal hump, by a waist allows free movement of the foot and the undeformed posture of the visceral sack with the stiff shell frame far from the substrate. The formation of the waist enforced the reduction of the number of gill-pairs in all derived conchiferan constructions.

(2.2.1.1.) Neopilinida.

The Neopilinida are flattened recent Monoplacophoran constructions with clear remnants of metamerism in the arrangement of muscles, nephridia and gills. So they must be early representatives of the transition phase to the Conchiferans. However, clear indications of reduction of metamerism from the anterior portion of the body become evident; the anterior gills are reduced and the muscle bundles fused (GUTMANN, 1974; EDLINGER, 1991a).

(2.2.1.2.) Evolution of Scaphopod constructions.

Scaphopods are derived from a Monoplacophoran stage with a posterior slit in the shell for the expulsion of faeces. A dorsoventral elongation of the construction caused the reduction of the number of muscles and gill pairs and the formation of a tube-like shell. The foot changes its form by a rearrangement of the internal muscle-lattice and becomes a burrowing organ. The posterior slit of the shell became an elongate hole. This hole enabled the animals to ventilate their mantle cavity when they penetrated into the substrate. The water is sucked in from the anterior region and expelled through the posterior hole. The total reduction of the gills is enforced by the narrowing of the mantle cavity when the elongate organisms developed (EDLINGER, 1991b) (Fig. 5).

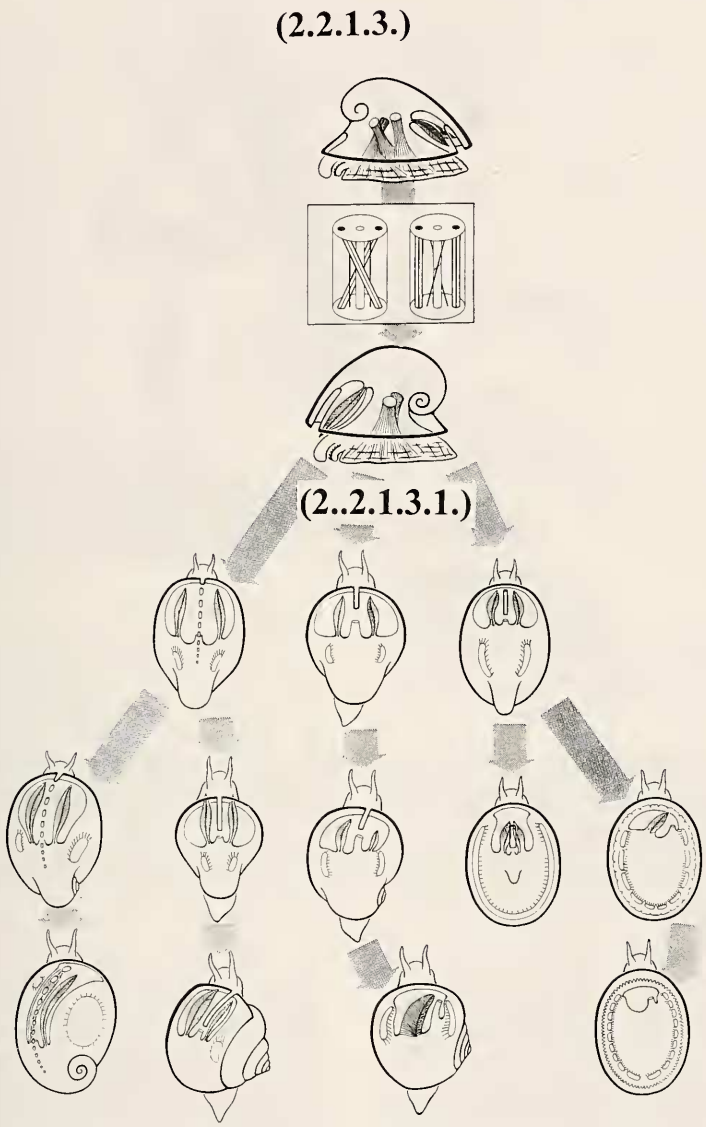

Figure 6. The evolution of the gastropod construction by torsion. Torsion occurs after the formation of a waist between the cephalopodium and the visceral hump and reduction of most of dosoventral muscles.

Figura 6. La evolución de la estructura de un gasterópodo mediante torsión. Ésta ocurre tras la formación de un estrechamiento entre el cefalopodio y el asa visceral, y la reducción de la mayoría de los músculos dorsoventrales.

(2.2.1.3.) Evolution of Gastropods (EDLINGER, 1988a, 1988b, 1989a).

The most significant event of gastropod evolution was the torsion of the visceral hump after a very narrow waist had formed and most of the gill pairs had been reduced. Torsion led to an anterior position of the partially reduced mantle ca-

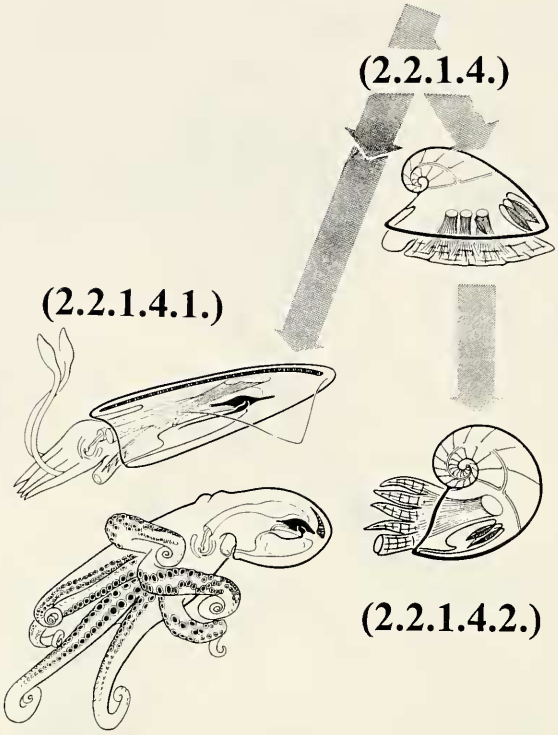

Figure 7. The evolution of cephalopods characterized by the appearance of gas-filled spaces at the top of the shell and by a radical rearrangement of the musculature of the cephalopodium with strong muscular arms and suckers.

Figura 7. Evolución de los cefalópodos, caracterizada por la aparición de cámaras llenas de gas en la parte alta de la concha y una redistribución radical de la musculatura del cefalopodio con fuertes ramas musculares y ventosas.

vity with the remaining gills and the formation of the chiasma of the lateral nerve cords. The precondition for torsion lies in a step by step reduction of dorsoventral muscle bundles of a Monoplacophoran ancestor and by narrowing of the waist between the cephalopodium and the visceral hump. This process is connected with a step by step spiralling up of the shell. The persistence of only one pair of crossing obliquely transversal muscles could cause the torsion. Totally bilaterally organised symmetric Bellerophontacean shells are representative of this process (Fig. 6).

(2.2.1.3.1) Radiation of Gastropod constructions: All gastropod lineages are derived from a Bellerophontacean stage with a bilateral and helical shell, which possessed slits or a series of holes in the posterior part of the shell for the expulsion of faeces. Only one pair of parallel dorsoventral muscles persisted. Asymmetry could arise by the partial or total reduction of one of the dorsoventral muscles and the change of the planispiral shell of Bellerophon-like ancestors to an asymmetric helical form. In most cases the gills became also unequal or one gill was entirely reduced (EDLINGER, 1988a, 1988b, 1989a).

Flattening and secondary reduction of the coil can result in the formation of a cup-like shell. Flattening must cause a change in the muscle arrangement. The dorsoventral muscles and their scares on the inner of the shells were enlarged to form

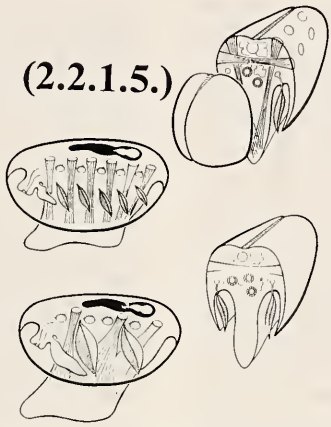

Figure 8. The evolution of bivalves by a rearrangement of the dorsoventral muscles and a division of the shell to a bivalve one.
Figura 8. Evolución de los bivalvos por medio de una redistribución de los músculos dorsoventrales y una división de la concha hacia una concha bivalva.

horseshoe-like insertions. The gills can persist as in *Fissurella*. In this case the retractor muscle will form a homogeneous horse-shoe-like entity. If the gills are also reduced and substituted by secondary gill-like structures the muscles are splitted up into a Monoplacophoran-like situation of *Patella* (EDLINGER, 1988a, 1988b, 1989a; HASZPRUNAR, 1988).

(2.2.1.4.) Evolution of Cephalopod constructions (BONIK, GRASSHOFF, GUTMANN AND KLEIN-RÖDDER, 1977). The development of gas-filled chambers in the apical part of the shell rendered the organisms more buoyant. The foot with its deformability and the adhesive capabilities was altered into a system of muscular arms with suckers which could grasp prey. Retraction of the soft-body into the shell inevitably caused expulsion of a water-current. In the course of evolution improvement of this mechanisms was altered into effective jet propulsion when the hind part of the foot was modified to form a narrow funnel through which the water expelled from the mantle cavity was concentrated to enhance the jet effect. This constructional situation can be observed in all cephalopods (Fig. 7). An early bifurcation or diphyletic development gave rise to the branches of endocochlean and exocochlean Cephalopod construction (2.2.1.4.1, 2.2.1.4.2).

(2.2.1.5.) Evolution of Bivalve Constructions (VOGEL AND GUTMANN, 1980). The origin of Bivalves can be understood as a rearrangement of the dorsoventral muscles in a high chambered Monoplacophoran ancestor. A considerable portion of the dorsoventrally and obliquely arranged muscles in the foot were shifted into a horizontal position connecting not the shell and the foot as in the former stages but the two laterally bent down plates of an evolving bivalved shell. Contraction of the muscles brought the flanks of the shells together in protective behaviour. Most of the vertical (dorsoventral) portions of the musculature retained their original retractile function in respect to the foot but the number of retractors was reduced. Consequently most of the gills disappeared with one pair remaining.

The remaining pair of gills are utilised as filterfeeding devices because lateral cephalic lobes bridged the gap between the mouth and the gills and formed conveyer belts for the transport of food from the gills to the mouth (Fig. 8).

DISCUSSION AND CONCLUSION

It is very obvious that in the perspective of constructional morphology and organismic evolution character-analysis and the establishment of sequences of organismic forms in the sense of homologies are inconclusive and arbitrary. They pose problems but do not provide answers because description of form and character analysis do not lead to constructional insight or an understanding of form determination. Constructional alteration in evolution can not reasonably be derived from genetic or other molecular features (GHISELIN, 1988; WÄGELE, 1994; WÄGELE AND WETZEL, 1994; EDLINGER, 1995). The understanding of organisms as constructions leaves no doubt that the constructional configuration determines evolutionary change of the living machinery and prescribes the sequence of constructional stages and of irreversible steps. There is little freedom for contingency in the order of the "bauplan" configurations and no encouragement for simple description and form comparison. Nothing useful can come from such traditional approaches which are blind to causal aspects and insensitive for explanatory principles.

When organisms are conceived as energy transforming constructions evolution must be ruled by constructional principles and not by subjective "gestalt" properties or subservient molecular mechanisms. As could be shown in the foregoing context strict obeisance of the constructional principles allows the rejection of constructionally impossible or improbable alternatives. From the methodology applied and the mode of reconstruction of the evolutionary transformations just advocated follows that traditional phylogenetic concepts, form sequences, and cladograms based on usual procedures are not considered valid. Therefore, traditional hypotheses are bypassed and left out of consideration when the criteria of the Frankfurt-Theory are applied. If somebody feels the need to adhere to the idea that Plathelminths, non-segmented worms, or Nemerteans might be the precursors of mollusc he or she should present a continuous model with a strict explanation of the intermediate constructional steps.

The genes and other molecular mechanisms which are subservient in relation to the living constructions and their structures have to comply with the constructional requirements and must follow constructional modifications of the machinery in the course of structural reorganisation. Taken as separate features molecular and physiological mechanisms are not useful for the elucidation of constructional change in evolution. Therefore, constructional morphology neglects all traditional suggestions as to the affinity of organismic groups based on form similarities in the sense of homologies and on subservient and constructionally dependent molecular and physiological properties.

It is not possible to give a list of all the published sequences of forms which were figured out to represent what all the authors tried to suggest as stages of mollusk evolution (SCHELTEMA, 1978; GÖTTING, 1980a, 1980b; HAAS, 1981; BANDEL, 1983; LAUTERBACH, 1983a, b; HASZPRUNAR, 1988, 1992a, b). Many contributions were formulated by paleontologists (RUNNEGAR AND POJETA, 1974; RUNNEGAR, POJETA, NOEL, TAYLOR, TAYLOR AND MCCLUNG, 1975; MAREK AND YOCHELSON, 1976; YOCHELSON, FLOWER AND WEBERS, 1973; POJETA JR., 1987) who started from one or the other fossilstructure. Most morphoclines presented since the last century are highly contradictory, however, all of them have in common an access that arbitrarily selects some features of skeletal or soft body structures.

Organisms as constructionally restrained and not deliberately transformable entities are not even expected. In none of the published morphoclines is the directionality of evolutionary transformation elaborated or explained as irreversible. Organisms are misconceived as shaped and freely modifiable pieces of art. Fruitful discussion can only start when alternative models with continuous explanations and well supported transformational polarities are given. In the present situation the discussion of all the morphoclines would require the sacrifi-

cium intellectus. Also in the field of radiation of the phylum Mollusca reconstructions have to be done on the consistent basement of constructional laws and solid criteria of directionality of evolutionary changes. In the recent only the models outlined above meet this conditions. All alternative concepts which will possibly appear must be discussed on the basis of this conditions.

REFERENCES

BANDEL, K., 1983. Wandel der Vorstellungen von der Frühevolution der Mollusken, besonders der Gastropoda und Cephalopoda. *Paläontologische Zeitschrift*, 57 (3/4): 271-284.

BEREITER-HAHN, J., 1991. Cytomechanics and biochemistry. In Schmidt-Kittler, N., Vogel, K. (Eds.): *Constructional morphology and evolution*. Springer Berlin-Heidelberg-New York: 81-90.

BONIK, K., GRASSHOFF, M. AND GUTMANN, W. F., 1977. Funktion bestimmt Evolution. *Umschau*, 77 (20): 657 - 668.

BONIK, K., GRASSHOFF, M., GUTMANN, W. F. AND KLEIN-RÖDDER, R., 1977. Die Evolution der Tintenfische, ein Entwurf für das Schaumuseum. *Natur und Museum*, 107 (8): 244-250.

EDLINGER, K., 1988a. Beiträge zur Torsion und Frühevolution der Gastropoden. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, 26: 27-50.

EDLINGER, K., 1988b. Torsion in Gastropods: A phylogenetical Model. *Malacological Review*, Suppl. 4: 239-248.

EDLINGER, K., 1989a. Zur Evolution der Schneckenkonstruktion I. - Torsion und Frühevolution der Prosobranchier. *Natur und Museum*, 119 (9): 272-293.

EDLINGER, K., 1989b. Sekundäre Wurmkonstruktionen bei amphineuren Mollusken. In Edlinger, K. (Ed.). *Form und Funktion - Ihre stammesgeschichtlichen Grundlagen*. Wiener Universitätsverlag, Wien, 196 pp.

EDLINGER, K., 1991a. The mechanical constraints in mollusc constructions - the function of the shell, the musculature, and the connective tissue. In Schmidt-Kittler, N. and Vogel, K. (Eds.): *Constructional morphology and evolution*. Springer Berlin-Heidelberg-New York: 359-374.

EDLINGER, K., 1991b. Die Evolution der Scaphopodenkonstruktion. *Natur und Museum*, 121 (4): 116-122.

EDLINGER, K., 1992a. Die "Unsichtbare Morphologie" - Energiefluß und Konstruktion. *Aufsätze und Reden der Senckenbergischen Naturforschenden Gesellschaft*, 39: 27-49.

EDLINGER, K., 1992b. Nervensysteme als integrale Bestandteile der mechanischen Konstruktion. *Aufsätze und Reden der Senckenbergischen Naturforschenden Gesellschaft*, 39: 131-155.

EDLINGER, K., 1994a. Morphologische Determinanten bei der Bildung von Nervensystemen. *Biologisches Zentralblatt*, 113: 25-32.

EDLINGER, K., 1994b. Das Spiel der Moleküle - Reicht das Organismusverständnis des molekularbiologischen Reduktionismus?-. *Natur und Museum*, 124 (6): 199-206.

EDLINGER, K., 1995. Organismen: Konstruktionen oder Genarrangements? *Biologisches Zentralblatt*, 114: 160-169.

EDLINGER, K., GUTMANN, W. F. AND WEINGARTEN M., 1991. *Evolution ohne Anpassung*. Verl. W. Kramer Frankfurt, 92 pp.

GHISELIN, M. T., 1988. The origin of molluscs in the light of molecular evidence. *Oxford Surveys of Evolutionary Biology*, 5: 66-95.

GÖTTING, K. J., 1980a. Origin and relationships of Mollusca. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, 18: 24-27.

GÖTTING, K. J., 1980b. Argumente für die Deszendenz der Mollusken von metameren Antezedenten. *Zoologisches Jahrbuch Anatomie*, 103: 211-218

GUTMANN, W. F., 1974. Die Evolution der Mollusken-Konstruktion: Ein phylogenetisches Modell. *Aufsätze und Reden der Senckenbergischen Naturforschenden Gesellschaft*, 25: 1-84.

GUTMANN, W. F., 1989. Die Evolution hydraulischer Konstruktionen. Organismische Wandlung statt altdarwinistischer Anpassung. *Senckenberg-Buch* 65, Verl. W. Kramer Frankfurt/M, 200 pp.

GUTMANN, W. F. AND EDLINGER K., 1994a. Organismus und Evolution - Naturphilosophische Grundlagen des Prozeßverständnisses. In Bien, G. and Wilke J. (Eds.): *Natur im Umbruch - Zur Diskussion des Naturbegriffs in Philosophie, Naturwissenschaft und Kunsttheorie*. Frommann-Holzboog, 109-140.

GUTMANN, W. F. AND EDLINGER K., 1994b. Molekulare Mechanismen in kohärenten Konstruktionen. In Maier, W. and Zoglauer, H. (Eds.): *Technomorphe Organismuskonzepte - Modellübertragungen zwischen Biologie und Technik*. Frommann-Holzboog, 128: 174-198.

GUTMANN, W. F. AND EDLINGER K., 1994c. Morphodynamik und Maschinentheorie: Die Grundlage einer kausalen Morphologie. In Gutmann, W. F., Mollenhauer, D. und Peters, D. St. (Eds.): *Morphologie und Evolution*. W. Kramer, Frankfurt/M: 177-199.

GUTMANN, W. F. AND EDLINGER K., 1994d. Neues Evolutionsdenken: Die Abkoppelung der Lebensentwicklung von der Erdgeschichte. *Archaeoteryx*, 12: 1-24.

HAAS, W., 1981. Evolution of calcareous hardparts in primitive molluscs. *Malacologia*, 21 (1-2). 403-418.

HASZPRUNAR, G., 1988. On the origin and evolution of major gastropod groups, with special reference to the streptoneura. *Journal of Molluscan Studies*, 54: 367-441.

HASZPRUNAR, G., 1992a. The first molluscs: small animals. *Bollettino Zoologico*, 59. 1-16.

HASZPRUNAR G., 1992b Preliminary anatomical data on a new neopilinid (Monoplacophora) from Antarctic waters. *Abstracts of the eleventh International Malacological Congress*, 307-308.

LAUTERBACH, K. E., 1983a. Erörterungen zur Stammesgeschichte der Mollusca, insbesondere der Conchifera. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, 21 (3): 201-216.

LAUTERBACH, K. E., 1983b. Gedanken zur Entstehung der mehrfach paarigen Exkretionsorgane von Neopilia (Mollusca, Conchifera). *Zeitschrift für zoologische Systematik und Evolutionsforschung*, 21 / 1: 38-52.

MAREK, L. AND YOCHELSON, E. L., 1976. Aspects of biology of Hyolitha (Mollusca). *Lethaia*, 9: 65-82.

POJETA, J. JR., 1987. Rostroconcha / Scaphopoda. In Cheetham, A. H. and Rowell, A. J. (Ed.): *Fossil Invertebrates*. Blackwell Scientific Publications, Palo Alto / Oxford / London / Edinburgh / Boston / Melbourne: 358-386.

RUNNEGAR, B. AND POJETA, J., 1974. Molluscan Phylogeny: The Paleontological Viewpoint. *Science*, 186: 311-317.

RUNNEGAR, B., POJETA J. JR., NOEL J., TAYLOR, J. E., TAYLOR, M. F. AND MCCLUNG, G., 1975. Biology of the Hyolitha. *Lethaia*, 8: 181-191.

SCHELTEMA, A. H., 1978. Position of the class Aplacophora in the phylum Mollusca. *Malacologia*, 17 (1). 99-109.

VOGEL, K. AND GUTMANN, W. F., 1980. The derivation of pelecypods: role of biomechanics, physiology and environment. *Lethaia*, 13: 255-264.

VOGEL, K., 1991. Concepts of constructional morphology. In Schmidt-Kittler, N. and Vogel, K. (Eds.): *Constructional morphology and evolution*. Springer Berlin-Heidelberg-New York: 55-68.

WÄGELE, J. W., 1994. Rekonstruktion der Phylogenese mit DNA-Sequenzen: Anspruch und Wirklichkeit. *Natur und Museum*, 124 (7): 225-232.

WÄGELE, J. W. AND WETZEL, R., 1994. Nucleic acid sequence data are not per se reliable for inference of phylogenies. *Journal of Natural History*, 94: 749-761.

YOCHELSON, E. L., FLOWER, R. H. AND WEBERS, G. F., 1973. The bearing of the new Late Cambrian genus *Knightoconus* (Mollusca: Monoplacophora) upon the origin of the Cephalopoda. *Lethaia*, 6: 275-310.